THE BRAINCASE AND ASSOCIATED STRUCTURES OF THE COTYLOSAUR REPTILE *PROCOLOPHON TRIGONICEPS* OWEN

By

T. S. Kemp

University Museum and Department of Zoology, Oxford

(With 1 plate and 5 figures)

Contents

Introduction

It is an extraordinary and unexplained fact that while the skull of the cotylosaurian reptile *Procolophon* is quite common in Lower Triassic Karroo deposits of South Africa, the braincase is almost always missing. Thus the description by Watson in 1914 of most of the skeleton, including the braincase, has remained practically the sole source of information about this part of the skull, although a figure and a very brief description of the ventral aspect has been published by Broili & Schröder (1936). Watson's description showed great insight for its time and remains, indeed, surprisingly modern. However, it lacks adequate illustration and certain aspects of the braincase were not visible in his material.

This present study is based upon a single, particularly large specimen of *Procolophon trigoniceps*, consisting of the skull, lower jaws and anterior part of the postcranial skeleton. It was collected by Dr F. R. Parrington in 1964 from Klipfontein, Bethulie, South Africa and forms part of his collection. Dr Parrington's collection has since been donated to the Museum of Zoology, Cambridge University where this particular specimen is housed, under the catalogue number **T** 1026.

Only the skull has been prepared so far. The matrix is a hard, red, fine sandstone which is barely affected by acetic acid. Thus preparation has been entirely mechanical, using a Burgess 'Engraver'. The dorsal roof of the skull has been weathered away with almost surgical precision, making it possible to prepare the braincase and the palate from the dorsal aspect as well as from the more conventional views. The postero-lateral part of the right side of the skull is also missing although the braincase of that side is complete. Distortion has

Ann. S. Afr. Mus. **64**, 1974: 11–26, 1 pl., 5 figs.

been slight and consists mainly of a degree of dorso-ventral crushing of the occipital region.

Description of the braincase and associated bones

Supraoccipital

The supraoccipital has suffered slightly from the dorso-ventral crushing but its form is clear. A narrow dorsal process runs postero-dorsally to make contact with the posterior edge of the skull table. It is triangular in section with a sharp median posterior edge and a flat antero-dorsal face. Ventrally the supraoccipital roofs over the posterior part of the brain cavity by means of a pair of wing-like lateral processes. Each of these processes is fairly thin (about 3 mm)

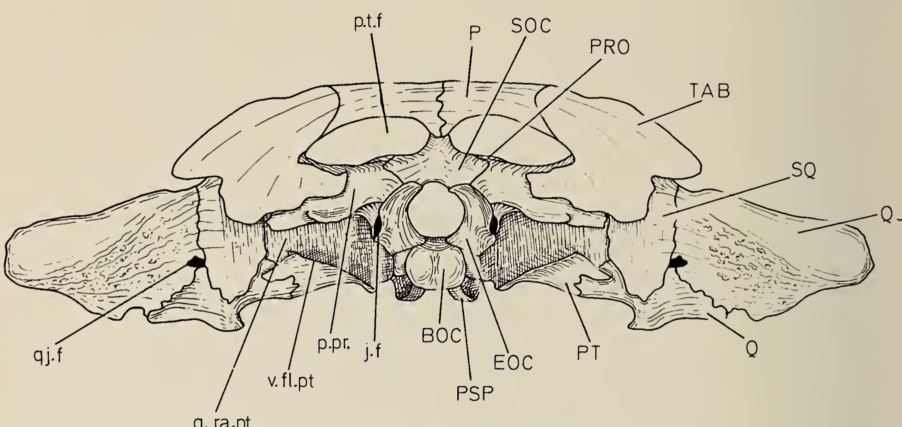

Fig. 1. *Procolophon trigoniceps* CUMZ T 1026.
Occipital view of skull, restored. × 1. For abbreviations see page 25.

but wide and lies in an approximately horizontal plane. The distal end contacts the prootic bone in front, the opisthotic extensively and the exoccipital posteriorly, and each of these respective sutures is in the form of a flush abuttment. A laterally directed ridge crosses the upper surface of each lateral process, in continuation of the sharp postero-dorsal edge of the paroccipital process. The anterior edge of the supraoccipital is slightly upturned and sharp.

Exoccipital

As a result of the slight downward displacement of the supraoccipital bone, the exoccipital of each side has been pushed a small degree backwards. On the right side the contacting faces of the supraoccipital and exoccipital have been exposed and are seen to be flat, buttressing surfaces of small extent. Below this suture the exoccipital is a narrow pillar, triangular in section, with a flattened lateral-facing surface. It is in contact with a posterior-facing facet of the opisthotic until, about half-way down the bone, they separate to form the large jugular foramen. Below the foramen contact between the exoccipital and the opisthotic is regained briefly so that the jugular foramen is entirely surrounded by those two bones.

The ventral region of the exoccipital expands, particularly laterally, so that it forms a broad base resting upon the postero-lateral corner of the basioccipital. As described by Watson (1914), two hypoglossal foramina lie near the ventral edge of the internal (intracranial) surface of the bone, but no external opening can be discerned and thus this specimen must be assumed to differ from Watson's in that the hypoglossal foramina open directly into the jugular canal.

Basioccipital

The occipital condyle is formed exclusively from the basioccipital and it is incipiently double, consisting of two low convexities separated by a medial cleft which together form a kidney-shape. Three ridges surround the ventral surface of the condyle, a pair of lateral ones and an anterior, transverse one. From the two points where these ridges meet, a pair of arm-like processes, separated from one another by a deep cleft, run forwards and slightly downwards to meet the parasphenoidal tubera and indeed to participate in the construction of these tubera.

The side of the basioccipital is vertical and high and makes flush contacts with the exoccipital and the para-basisphenoid. A process of the opisthotic overlies it postero-dorsally. A sharp longitudinal ridge runs backwards across the lateral basioccipital surface from the level of the tubera and turns slightly dorsally just in front of the exoccipital, finally to be continued across the base of the latter bone right to the anterior margin of the jugular foramen.

The dorsal surface of the basioccipital is constricted posteriorly by the exoccipitals but further forwards it forms a broad floor to the braincase, slightly concave from side to side. A low median ridge is present.

Para-basisphenoid

Although the basisphenoid cannot be distinguished from the parasphenoid by suture, the surface texture seems to indicate which part is dermal bone and which endochondral.

The paired tubera formed by the parasphenoid together with the basioccipital are massive, narrow and are separated by a very deep cleft. From the tip of each tuber there runs forwards a rounded ridge which rapidly loses height until it merges with the swelling of the basipterygoid process. The basipterygoid process itself faces antero-laterally and fits into the deep socket in the pterygoid (as described by Parrington 1962) as an apparently kinetic joint. A very slender processus cultriformis arises medially between the basipterygoid processes and runs steeply upwards. Its ventral surface is convex from side to side and it narrows evenly to a sharp point.

The huge size of the tubera may be appreciated in lateral view. The posterior surface of each tuber is deeply hollowed out and, since the tuber expands laterally a little compared to the basioccipital, there are a pair of high, narrow concavities facing freely posteriorly and presumably being the sites of attachment of a pair of muscles. Above the level of the tubera, the parasphenoid runs postero-laterally as an otic process which reaches to the level of the fenestra ovalis, although it does not appear to have participated in the true margin of the fenestra as the rest of the margin is formed by unfinished bony lips which must have been covered by a cartilage layer in life. The parasphenoid has no such lip, and it is most probable that an unossified part of the basisphenoid lay immediately internal to the parasphenoid and formed the actual margin of the fenestra ovalis. The otic process of the parasphenoid is continued anteriorly as a broad, rounded ridge all the way to the basipterygoid process. The endochondral, basisphenoidal part of the complex rises as a delicate, less well-ossified vertical sheet of bone above this ridge. It forms the actual sidewall of the braincase and is in sutural contact with the anterior end of the prootic. However, between the prootic, the basisphenoid and the otic process of the

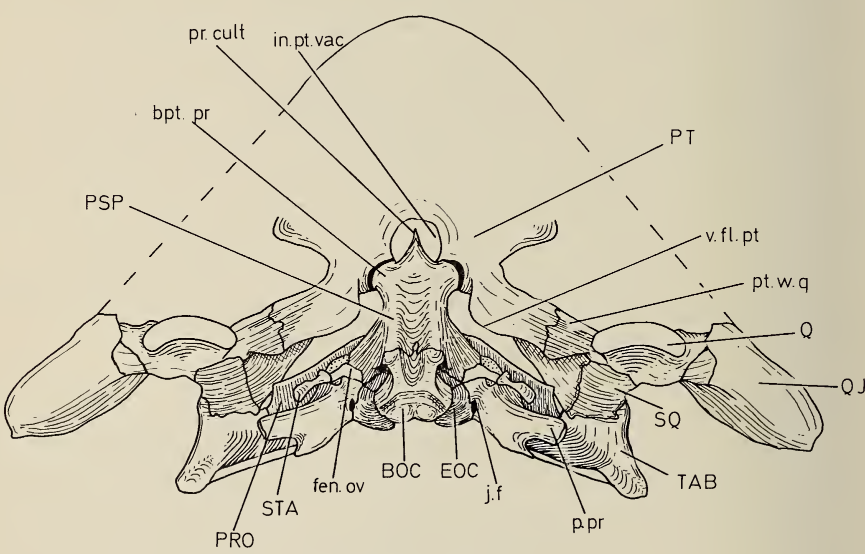

Fig. 2. *Procolophon trigoniceps* CUMZ T 1026.
Ventral view of the posterior part of the skull. × 1.

parasphenoid, the sidewall of the braincase is unossified, leaving a fairly large aperture anterior to the fenestra ovalis. The side of the basisphenoid gradually merges anteriorly with more compact, well-ossified bone until by the level of the basipterygoid process the parasphenoid part of the complex has apparently completely taken over.

The dorsal surface of the basisphenoid has been exposed completely on the left side of the skull. The posterior part continues the braincase floor forwards from the basioccipital although these two bones are separated by a narrow unossified zone. The sides of the braincase too are formed from the basisphenoid, in continuity with the prootic. However, the sides converge and after a very short distance they turn medially to form the vertical dorsum sellae. This structure is thus composed exclusively of the basisphenoid bone. The sella turcica is a very large, deep pit, divided by a thin median septum in its

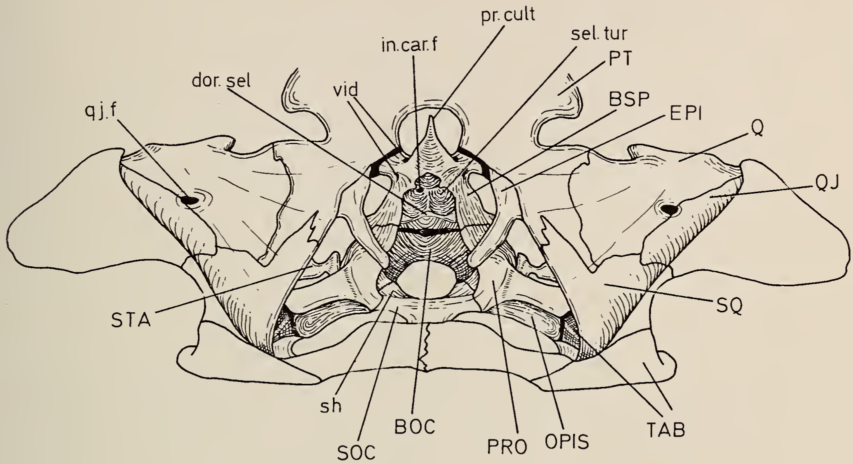

Fig. 3. *Procolophon trigoniceps* CUMZ T 1026.
Anterodorsal view of the posterior part of the skull. × 1.

posterior part. The more anterior part of the sella lacks the septum and its floor slopes quite steeply upwards to end abruptly at the base of the processus cultriformis. A medially directed spur of the basisphenoid slightly constricts the anterior part of the sella on either side.

As Watson (1914) suspected, a vidian canal pierces the basipterygoid process. The posterior foramen opens immediately behind and above the basipterygoid process and the anterior foramen is to be found above the anterior part of the process. That these two foramina do indeed connect with one another is shown by a break on the right side through the canal itself. An internal carotid foramen emerges on the left side of the sella turcica in the region referred to as the anterior part. Whether or not there is a corresponding foramen on the right side is unknown since this side has not been prepared (for the sake of the strength of the specimen).

The dorsal surface of the basipterygoid process is divided by a ridge into antero-dorsal and postero-dorsal faces. The ridge continues medially and antero-dorsally to form the lateral edge of the processus cultriformis. The upper surface of the processus itself is broadly concave from side to side.

Opisthotic

The sutures between the opisthotic and the other bones of the braincase are all clearly distinguishable. The medial end forms a long suture with the supraoccipital, behind which the opisthotic turns to form a posterior facing facet which is in contact with the exoccipital, as described. The massive paroccipital process is formed from both the opisthotic and the prootic. The opisthotic part runs horizontally and somewhat posteriorly and slightly ventrally, as a very well-developed process. The dorsal surface is deeply concave and it gradually widens laterally. It is marked off from the posterior surface by a high, narrow ridge which continues the line of a much less marked ridge on the supraoccipital. The posterior surface of the paroccipital process is smooth and bears a horizontal shelf along most of its ventral edge. The upper part of the distal end of the posterior surface is overlapped by a process of the tabular bone. The ventral surface of the paroccipital process is smoothly rounded and is continuous with the ventral surface of the shelf referred to above. The distal end of the process ends freely as an unfinished bone surface that presumably remained cartilage-covered in life. The only direct contact of the opisthotic in the region of the distal end of the paroccipital process is with the tabular bone, so far as can be ascertained in the slightly damaged case of this specimen, by means of the overlap of its posterior surface noted above.

The anterior surface of the paroccipital process is smoothly concave from top to bottom, forming as it does the posterior wall of the middle ear cavity. The upper part is in contact with the prootic over much of its length as described below. Ventral to the prootic, the opisthotic sends a process antero-medially which contacts the basal region of the exoccipital and the side of the basioccipital. The upper part of this process bears a lip of unfinished bone which makes the postero-ventral rim of the fenestra ovalis. The lower part contributes the posterior margin of the jugular foramen. Between the fenestra ovalis and the jugular foramen, the opisthotic process is strongly concave and carries a small foramen.

Prootic

The prootic meets the supraoccipital along a short suture at its postero-medial extreme. A second contact between these two bones occurs at a slightly more ventral level, because a horizontal shelf extends medially from the prootic into the brain cavity, about 1 mm below the dorsal edge of that bone. The shelf meets a similarly developed shelf arising from the antero-lateral face of the supraoccipital. It seems likely that the shelf marks the area of contact of the persistently cartilaginous taenia marginalis of the chondrocranium, as implied by Price (1935) for a similar structure in *Captorhinus*.

A slight ridge marks the medial part of the prootic, which forms the braincase wall, from the paroccipital process of the prootic, which extends laterally in contact with the opisthotic. The inner part of the prootic is in the same plane as the adjacent opisthotic, but laterally it twists to form a horizontal shelf in contact with the dorsal edge of the more or less vertical opisthotic. Thus the prootic constitutes a definite roof over the middle ear cavity, extending as far laterally as does the opisthotic which forms the hind wall of the cavity. The distalmost part of the prootic actually contacts the quadrate ramus of the pterygoid although no suture seems to form.

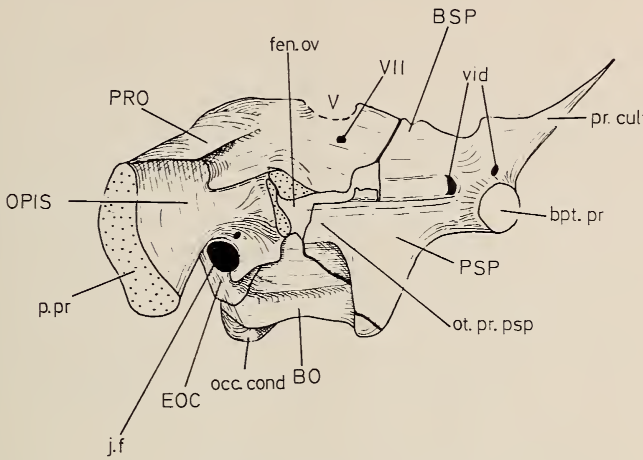

Fig. 4. *Procolophon trigoniceps* CUMZ T 1026.
Right lateral view of the braincase, with certain details added from the left side. × 2.

In front of the paroccipital process, the prootic expands to form a broad, thin sheet making the sidewall of the braincase. A lip of unfinished bone on the ventral edge constitutes the dorsal margin of the fenestra ovalis, while half-way up the bone is a foramen which presumably transmitted the facial nerve (VII). The dorsal edge of the prootic of both sides has been slightly damaged and obscured by the epipterygoid collapsing across it. It appears to bear a notch of some sort exactly where the epipterygoid lies, and if this is true, then it would be reasonable to suppose that such a notch marks the region of exit from the cranial cavity of the trigeminal nerve (V).

The internal surface of the prootic could not be widely exposed in this specimen. The anterior part is certainly well ossified but posteriorly, at the level of the paroccipital process, ossification seems to have been absent, in relation to the formation of the inner ear structures.

Stapes

The left stapes is perfectly preserved and is at least approximately in its correct position with the proximal end adjacent to the fenestra ovalis. It is surprisingly small, about 6 mm in length. The proximal end is swollen and roughly triangular in end-on view, and it narrows rapidly but smoothly into the very slender shaft. The distal end is expanded asymmetrically into a broad but very thin plate. The ventral surface (as oriented in the specimen) is slightly convex from anterior to posterior edges and the posterior edge continues the line of the shaft of the bone. Apart from the proximal surface, the whole bone is formed from well-ossified, finished bone and does not appear to have suffered any damage. Neither stapedial foramen nor dorsal process is present.

Quadrate

The narrow, kidney-shaped articulating surface of the quadrate condyle is oriented transversely with the convex edge at the front. It faces very slightly forwards and is gently concave from side to side. Above the condyle the medial part of the quadrate expands to form a very extensive but thin pterygoid wing, which is plastered on to the anterior surface of the quadrate ramus of the pterygoid and also contacts both the squamosal and the quadratojugal bones. In posterior aspect the pterygoid wing of the quadrate is hidden by the underlying pterygoid meeting a large ventral extension of the squamosal, the latter itself also a thin sheet of bone in contact with the back of the quadrate. Only the ventral part of the quadrate is visible and is seen to form a suture with the lateral end of the ventral flange of the pterygoid (described below). There is no distinct boss on the quadrate in this region of this particular specimen, unlike the case of the specimen described by Parrington (1962).

Lateral to the condyles the quadrate has the form of a thick, stout process which buttresses powerfully against the quadratojugal, the latter bone extending a little way medially behind the quadrate to further strengthen this contact. The quadratojugal foramen lies in the suture between the quadrate and the quadratojugal above the middle of the condyle. In posterior view the foramen is actually bounded medially by the ventral process of the squamosal.

Pterygoid

The deep sockets for reception of the basipterygoid processes appear to face postero-medially and to have the form of more or less hemispherical cups, as described by Parrington (1962). Immediately behind and lateral to them, the quadrate rami of the pterygoids arise as broad, thin sheets of bone. Each one is extensively overlain by the quadrate as described, and also by a long spur of the squamosal lying along the dorsal region. The postero-ventral surface of the pterygoid is, however, more or less completely exposed. It carries a well-developed crest along its antero-lateral margin which is horizontal at its front end but gradually twists until it is approaching a vertical plane by the time it sutures with the quadrate.

Epipterygoid

The epipterygoids of both sides are present but have been distorted so that they apparently lie more horizontally than in life. The base of each one is a thin, broad sheet of bone plastered against the lateral face of the pterygoid. The ascending process is narrow and typically reptilian.

Quadratojugal

The extraordinary postero-lateral extension of the quadratojugal of *Procolophon* is of course well known. The medial connections of the bone are with the quadrate as described and also with the ventral process of the squamosal behind the quadrate The posterior face is sculptured in a manner suggestive of superficial dermal bone and not at all in keeping with attachment of muscles or other soft parts.

Squamosal

The small component of the squamosal that lay on the skull roof has weathered away but two internal processes remain. An anterior process overlies the dorsal edge of the quadrate ramus of the pterygoid, and a ventral process, in the form of a flat sheet, runs down over the back of the quadrate as described earlier by both Watson (1914) and Parrington (1962). It is in contact with the medial edge of the quadratojugal for most of its height. From the dorso-medial part of the squamosal where the two processes meet, the bone turns medially and runs along the anterior face of the occiput, presumably to the parietal. This part is completely covered behind by the tabular.

Tabular

Again, most of the dorsal part of this bone has been lost by weathering. Anteriorly the tabular forms a strong buttressing suture with the squamosal, a connection which would have been obscured had the skull roof been present. From here the tabular curves ventrally becoming thinner, and medially it covers the dorso-lateral part of the paroccipital process. The lateral part is produced as the triangular tabular 'horn', which bears a distinct groove on its ventral surface. The groove runs from the distalmost tip of the bone along its posterior edge, in an antero-medial direction, to disappear at the level of the ventral occipital process of the tabular.

Discussion

As members of the cotylosaur reptiles, the procolophons are involved in the debate about the interrelationships of early tetrapods, despite their relatively late occurrence, and in this context the most important regions of the skull are the middle ear, the braincase (particularly the otic region) and the pattern of bones in the temporal region (see Panchen 1972 for a recent review). Since the latter part of the skull of procolophons is so specialized while the former two parts have hitherto remained poorly known, it is not surprising that the phylogenetic position of this group is still unclear. Olson (1965) succinctly indicated the general possibilities as twofold. In the first place it is possible that the procolophonids, with or without their putative relations the pareiasaurs, arose directly from the seymouriamorph amphibian complex independently of the captorhinomorphs. This opinion has been held tentatively by Parrington

(1962) on the basis of the temporal bones, and by Daly (1969). In the second place, the procolophons may be a very early divergence from primitive but recognizably captorhinomorph reptiles, a view associated with Romer (1968) and, less confidently, Carroll & Gaskill (1971).

We may now consider what bearing the present study has upon this problem.

Middle ear

The position of the fenestra ovalis is typically reptilian and there is no development of a tube-like extension of the parasphenoid and otic bones carrying the fenestra laterally as in seymouriamorphs (White 1939). The lateral expansion of the parasphenoid at the level of the middle ears is in fact no more extensive than in *Captorhinus* (Price 1935) or *Sphenodon* for example.

The position of the tympanic membrane, always assuming it was present, is problematical. Since the time of Watson (1914) stress has been laid on the otic notch of *Procolophon* and its allies, by which was meant the posterior margin of the quadrate along with the corresponding concavity in the superficial dermal bones. In fact the situation is less simple because in the procolophonids secondary extension of the tabular and the quadratojugal has resulted in a large semicircular notch in the posterior margin of the skull roof, which has a marked but superficial similarity to the otic notch of the labyrinthodonts. This secondary, dermal notch does not reflect at all closely the form of the underlying primary otic notch. While Romer (1956, 1968) uses the term 'otic notch' for the primary notch, Colbert (1946) and Parrington (1962), among others, use the term for the secondary notch, and the implication is that these two usages of 'otic notch' refer to two different possible positions for the tympanic membrane.

There are good reasons for doubting that the tympanum lay within the secondary, dermal notch. Particularly, the stapes of the present specimen lies approximately in its natural position with its swollen footplate more or less in contact with the fenestra ovalis, yet its undamaged distal end lies a relatively huge distance from the dermal notch (Figure 2; Plate 1). In order to reach the notch, a cartilaginous extrastapes some 15 mm in length would have been necessary. This represents 250% of the length of the stapes and seems most unlikely on mechanical grounds, and there is no modern reptile known which has such an arrangement (Baird 1970).

The actual edges of the dermal notch give no indication that they supported any part of a tympanic membrane. The edges of the tabular and the squamosal are smoothly rounded, while that of the quadratojugal is sculptured in the manner of the rest of the superficial dermal bones, which does not suggest the presence of soft tissues. It would seem therefore that the tympanum did not lie within this dermal notch, although it remains possible that the notch marks the outer opening of an external auditory meatus which led internally to the ear drum.

PLATE 1. *Procolophon trigoniceps* CUMZ T 1026.
Stereophotographs of the skull, natural size. Above, ventral and slightly posterior view; below, occipital view. (Photographs by Mr William Lee.)

If the stapes is to be taken as a guide, the tympanum must have been somewhere around the distal end of the paroccipital process, which in turn is posterior to the medial part of the quadrate. There are no markings on the bones of this region so the precise position can only be guessed, but in any case this represents a generally reptilian, post-quadrate position.

The stapes itself is specialized from the presumed primitive condition by the absence of both stapedial foramen and dorsal process. Regarding the latter, it is possible that the expanded distal end of the bone represents a broad dorsal process, although there are no serious indications of this. It is difficult to see how such a process could have contacted the paroccipital process, for example. The generally small size, delicacy and abrupt expansion of its foot-plate all give the stapes a rather 'sauropsid' appearance (Olson 1966; Baird 1970).

The tympanic cavity too, as far as can be judged from its osteological features, has the arrangement of a 'sauropsid' reptile like *Sphenodon* or the lizards. The manner in which the prootic contributes to the roofing of the cavity at the level of the top edge of the paroccipital process, and the extensive anterior limit formed by the quadrate ramus of the pterygoid, support such a comparison, which can be extended, too, to *Captorhinus*.

Thus the evidence of the middle ear structure points towards a true reptilian affinity of *Procolophon*, rather than to a particular relationship with the seymouriamorphs, despite certain difficulties in the form of the stapes and the absence of a clear-cut indication of the position of the tympanum. In fact, it would not be surprising for loss of the tympanum to have occurred, a common phenomenon amongst modern squamates (Baird 1970).

Braincase

The form and relations of the paroccipital process are often used to distinguish between labyrinthodonts (including seymouriamorphs) and reptiles. In the labyrinthodonts the paroccipital process runs dorso-laterally and contacts the tabular bone at its distal end, thus forming a brace between the skull roof and the basis cranii. The supraoccipital is usually unossified. In contrast, the reptilian paroccipital process typically runs laterally to contact the suspensorial (squamosal-quadrate) region of the skull, bracing of the roof to the basis cranii involving a well-ossified supraoccipital bone.

In the case of *Procolophon*, the paroccipital process has a perfectly reptilian form and it extends laterally towards the suspensorial region; and a well-developed supraoccipital bone, closely similar to that of *Sphenodon* for example, is present. The difficulty is that the distal end of the paroccipital process is in contact with the tabular bone, and fails to reach the squamosal or quadrate, and thus the technical reptilian requirement is not met. However, the temporal region of the *Procolophon* skull is extremely modified from the primitive tetrapod condition, and in particular the quadrate bone is much further forwards, the squamosal reduced and the tabular (if indeed this bone is correctly homologized) greatly enlarged and extended on to the occipital surface. It is not safe therefore to assume that the failure of the paroccipital process to contact the squamosal and/or the quadrate is anything more than a further manifestation of the extensive remodelling of this part of the skull.

The processus cultriformis of the parasphenoid of *Procolophon* is very much reduced compared to that of *Seymouria* (White 1939) or *Kotlassia* (Bystrow 1944), a feature in which it resembles all typical reptiles.

Like the middle ear, the structure of the braincase is essentially reptilian but shows certain peculiarities, in this case the relation of the distal end of the paroccipital process to the rest of the skull.

Primitive procolophons

The strongest arguments for relating procolophons directly to seymouriamorphs are based on certain forms which combine some of the procolophonid

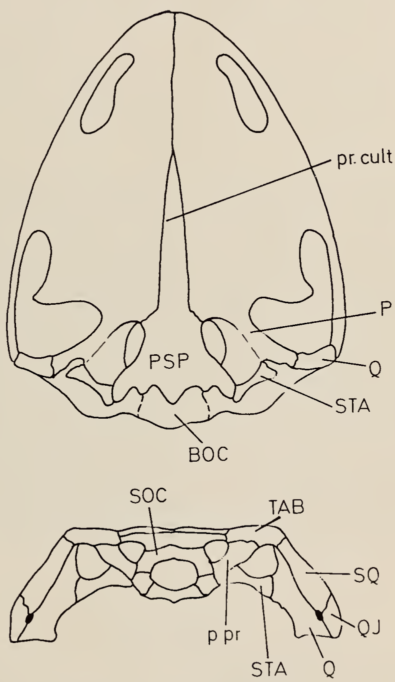

Fig. 5. *Nyctiphruretus acudens*.
Skull in ventral and occipital views to show braincase and stapes. Natural size. (Redrawn from Efremov 1940.)

specializations with seymouriamorph characters. The most important is *Nyctiphruretus* (Fig. 5) from the Upper Permian of Russia (Efremov 1940) which shows shortening of the jaw length, reduction of the skull table coupled with loss of the supratemporal, relatively huge orbits and an enlarged pineal foramen. These *Procolophon*-like characters are however associated with a seymouriamorph-like braincase in which the paroccipital processes extend dorsolaterally to make firm contact with the tabulars at the postero-lateral corners of the skull. The tabulars do not extend down the occipital surface. Also like the seymouriamorphs, the processus cultriformis is unreduced. On the other hand, the middle ear is peculiar for there is no otic notch in the rear margin of the skull roof and the stapes runs ventro-laterally from the fenestra ovalis to a firm contact with the quadrate, and thus this part of the skull resembles neither *Procolophon* nor the seymouriamorphs. Clearly convergence has occurred. If *Nyctiphruretus* does link *Procolophon* directly to the seymouriamorphs, then *Procolophon* has achieved a reptile-like braincase and ear independently of captorhinomorphs. If *Nyctiphruretus* and *Procolophon* are related and are descended from true reptiles, then the braincase of *Nyctiphruretus* has converged upon the structure of the seymouriamorph braincase. And if *Procolophon* is a captorhinomorph derivative, while *Nyctiphruretus* is a seymouriamorph, then the similarities between these two genera have arisen independently, presumably in relation to the adoption of a similar mechanical jaw function. As long as it is held that braincase and middle ear structure are the best guides to lower tetrapod phylogeny, the latter hypothesis will remain the most attractive.

None of the other supposed primitive procolophons help in this problem. *Nycteroleter*, also from the Russian Upper Permian (Efremov 1940), is even more seymouriamorph-like with its dorsal otic notch. The Upper Permian form *Owenetta*, from South Africa (Broom 1939), has a skull roof which appears to be ideally primitive procolophonid but unfortunately nothing is yet known about the details of its braincase.

The recent description of a Lower Permian tetrapod *Acleistorhinus* by Daly (1969) as a primitive procolophon has been doubted by Carroll & Gaskill (1971) and receives no support from the present work. The extraordinary structure of the braincase and stapes of *Acleistorhinus* only serve to highlight the unremarkably reptilian-like form of the corresponding structures in *Procolophon*.

Summary

A detailed, bone by bone description of the braincase, stapes, pterygoquadrate and parts of the quadratojugal, squamosal and tabular of a large specimen of *Procolophon trigoniceps* is given.

The middle ear, paroccipital process and processus cultriformis are all basically reptilian in form, and point towards a captorhinomorph ancestry of procolophons, rather than their direct derivation from seymouriamorphs.

Nyctiphruretus is problematical and may resemble the procolophonids by convergence, being itself a seymouriamorph.

Acknowledgements

My thanks must go particularly to Dr F. R. Parrington, F.R.S., for his continued interest and encouragement, and for the initial loan of the specimen. Dr K. A. Joysey has kindly allowed me to retain the specimen on loan from Cambridge University Museum of Zoology. I am grateful to Mr William Lee for undertaking the photography associated with this work.

References

Baird, I. L. 1970. The anatomy of the reptilian ear. *In*: gans, c. & parsons, t. s., *eds. Biology of the Reptilia.* **3**: 193–275. London; New York: Academic Press.

Broili, F. & Schröder, J. 1936. Beobachtungen an Wirbeltieren der Karrooformation. xxi. Über *Procolophon* Owen. *Sber. bayer. Akad. Wiss.* **1936**: 239–256.

Broom, R. 1939. A new type of cotylosaurian, *Owenetta rubidgei. Ann. Transv. Mus.* **19**: 319–321.

Bystrow, A. P. 1944. *Kotlassia prima* Amalitzky. *Bull. geol. Soc. Am.* **55**: 379–416.

Carroll, R. L. & Gaskill, P. 1971. A captorhinomorph reptile from the Lower Permian of Europe. *J. Paleont.* **45**: 450–463.

Colbert, E. H. 1946. *Hypsognathus,* a Triassic reptile from New Jersey. *Bull. Am. Mus. nat. Hist.* **86**: 229–274.

Daly, E. 1969. A new procolophonoid reptile from the Lower Permian of Oklahoma. *J. Paleont.* **43**: 676–687.

Efremov, J. A. 1940. Die Mesen-Fauna der permischen Reptilien. *Neues Jb. Miner. geol. Paläont.* (Abt. B) **84**: 379–466.

Olson, E. C. 1965. Relationships of *Seymouria, Diadectes* and Chelonia. *Am. Zool.* **5**: 295–307.

Olson, E. C. 1966. The middle ear—morphological types in amphibians and reptiles. *Am. Zool.* **6**: 399–419.

Panchen, A. L. 1972. The interrelationships of the earliest tetrapods. *In*: joysey, k. a. & kemp, t. s., *eds. Studies in vertebrate evolution*: 65–87. Edinburgh: Oliver & Boyd.

Parrington, F. R. 1962. Les relations des cotylosaures diadectomorphes. *Colloques int. Cent. natn. Rech. scient.* **104** (*Problèmes actuels de paléontologie*): 175–185.

Price, L. I. 1935. Notes on the braincase of *Captorhinus. Proc. Boston Soc. nat. Hist.* **40**: 377–386.

Romer, A. S. 1956. *Osteology of the reptiles.* Chicago: University of Chicago Press.

Romer, A. S. 1968. *Notes and comments on vertebrate paleontology.* Chicago; London: University of Chicago Press.

Watson, D. M. S. 1914. *Procolophon trigoniceps,* a cotylosaurian reptile from South Africa. *Proc. zool. Soc. Lond.* **1914**: 735–747.

White, T. E. 1939. Osteology of *Seymouria baylorensis* Broili. *Bull. Mus. comp. Zool. Harv.* **85**: 325–409.

Abbreviations

BOC—basioccipital
bpt.pr—basipterygoid process
BSP—basisphenoid
cond—condyle
dor. sel—dorsum sellae
EOC—exoccipital
EPI—epipterygoid
fen. ov—fenestra ovalis
in. car. f—internal carotid foramen
in. pt. vac—interpterygoid vacuity
j.f—jugular foramen
occ. cond—occipital condyle
OPIS—opisthotic
ot. pr. psp—otic process of the parasphenoid
p. pr—paroccipital process
pr. cult—processus cultriformis
P—parietal
PRO—prootic
PSP—parasphenoid
PT—pterygoid
p.t.f—post-temporal fenestra
pt. w. q—pterygoid wing of the quadrate

Q—quadrate
QJ—quadratojugal
qj. f—quadratojugal foramen
q. ra. pt—quadrate ramus of the pterygoid
sel. tur—sella turcica
sh—shelf for cartilaginous taenia marginalis
SOC—supraoccipital
SQ—squamosal
STA—stapes
TAB—tabular
V—notch for the trigeminal nerve
vid—opening of the vidian canal
v. fl. pt—ventral flange of the pterygoid
VII—foramen for the facial nerve